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REVIEW

Cinnamate and cinnamate derivatives in plants

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Abstract Cinnamic acid, an ubiquitous alpha beta unsaturated acid, upon hydroxylation yields *p*-hydroxy cinnamic acid or *p*-coumarate, a plant mono phenol. Being, precursor for the production of various di (lignans), polyphenols (lignins) and also substituted derivatives, it seems to be an important aromatic chemical in growth and development of plants. This aromatic chemical substance synthesized primarily by almost all forms of plants, seemingly involves in the regulation of various physiological processes. The presence of this ubiquitous plant alpha beta unsaturated acid and its derivatives have been adopted by plants for various mechanisms. An effort towards the consolidation of these is made here.

Keywords Plant phenolics · Phenylpropanoids · Cinnamic acid · Cinnamate derivatives · Ubiquitous presence

Cinnamic acid

Cinnamic acid (CA) and its hydroxy derivative, synthesized with aromatic amino acids—phenylalanine and tyrosine—comprises a large family of organic acid isomers mostly of plant origin or synthesized in the laboratory or manufactured industrially. Various flavonoid pigments and polymer tannins produced primarily due to combinations of cinnamate and benzoate derivatives are chiefly responsible for imparting specific colour and flavour to a vintage wine (Jitareanu et al. 2011). The phenolic compound that gives oil of cinnamon its characteristic odor and flavor is cinnamic acid. CA, also known as phenylacrylic acid, forms monoclinic crystals, such as needles or prisms having melting and boiling point of 133 and 300 °C, respectively. By structure the molecule is composed of 9 carbon, 8 hydrogen, and 2 oxygen atoms (Zhiqui et al. 2003). The phenol mimics the flavor of spice of cinnamon (Anslow and Stratford 2000) and also, demands controlled storage conditions. Temperature, light, and pH need to be kept constant to ensure the quality (Davidson et al. 2005). The pH is reported to affect the solubility of CA and also the derived flavonoids. Because of being dissociated, CA is more soluble in an alkaline environment (higher than its pK_a). CA and its derivatives are reported to have antimicrobial cum antifungal activities (Davidson et al. 2005; Lone et al. 2014). It is also reported that it uncouples the energy transducing membrane thereby stimulates non-specific membrane permeability. This allows proton influx across the plasma membrane (Chambel et al. 1999). CA being a phenol characteristically kills microorganisms like that of a typical phenol or cresol, which are known to affect membrane permeability and also interfere with enzyme function. This therefore, also affects the metabolic pathways associated with energy production (Technology 1998). CA and vanillin might remain in soil after release from the root of *Solanum melongena* (egg plant) despite root removal (Chen et al. 2011). While Ding et al. (2007) and Shuab et al. (2013) reported autotoxicity due to higher concentrations of CA in the *Cucurbita ficifolia* seedlings (fig leaf gourd) and *Cucumis sativus* cotyledons. Chen et al. (2011) too reported autotoxicity due to

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high CA concentration in the *S. melongena,* hence producing an elevated susceptibility to infections causing disease. CA at 5 mg/L increased the height of plants in *Magorana hortensis* and at 10 mg/L significantly increased oil percentage, total oil yield and sugar content per plant (El-Moursi et al. 2012). Lower cinnamate concentrations increase in vivo nitrate reductase activity and total protein content (Singh et al. 1997). However, higher concentration proved inhibitory. CA is a plant production promoter, as a lasting-effect fungicide, high yield, corrosion prevention and freshness preservation of fruits and vegetables. It has extensive applications, but the consumption in the domestic market is very small today. With the development of the aspartame, production and the expansion of its consumption sectors, the consumption of L-phenylalanine will become brisk and the CA production will be promoted. The demand of L-phenylalanine in the world is around 15,000 tons a year, needing 23,000 tons of CA. The demand of L-phenylalanine in China is around 2000 tons a year, needing around 3000 tons of cinnamic acid. The output of cinnamic acid in China is only less than 1000 tons today and the deficit has to be bridged by imports. Unfortunately the cited author has not been able to source such a data for commerce in India vis-a-vis CA or L-phenylalanine (CNCIC 2006)! Last 10–15 years have seen an accelerated interest of food scientists in hydroxycinnamates due to their being components of bioactivity in human diet, since these comprise important structural cum functional entities of plant cell wall. These also act as precursors (*p*-coumarate, caffeate, ferulate, sinapate) for synthesis of food flavouring agents. Norwich (UK) hosted Ferulate '98' conference from July 9 to 11, 1998. There were five sections: hydroxycinnamates in food—role in nutrition and health; hydroxycinnamates in plant cell walls; biosynthesis of hydroxycinnamates; enzymology of biosynthesis and degradation; exploitation of hydroxycinnamates. In their review the then current state-of-the-art was discussed and provided suggestions for future research that arose from this conference.

Biosynthesis

Shikimic acid is the base precursor for polyphenols in all higher plants, this pathway is uniquely restricted to plants, bacteria and some marine animals (Chen et al. 2006a, b; Vanholme et al. 2012a, b; Chen et al. 2012) (Fig. 1). Plant natural products like phenylpropanoids are important for plant, human and animal health (Dixon and Sumner 2003; Sharma 2011). Erythrose-4-phosphate and phosphoenolpyruvate (PEP), both products of the general carbohydrate metabolism, enter the shikimate pathway to produce aromatic amino acids tyrosine, phenylalanine and tryptophan (Orcaray et al. 2011; Corea et al. 2012). However, it is the earlier two amino acids which on deamination introduce a double bond in the non-aromatic part, by enzymes phenylalanine ammonia lyase (PAL) yield cinnamic acid (CA) and tyrosine ammonia lyase (TAL) which yields *p*-hydroxy cinnamic acid directly. Phenylalanine ammonia lyase (PAL: EC4.3.1.5) qualifies for being first enzyme in the phenylpropanoid biosynthesis pathway (Dixon and Lamb 1990). One more enzyme cinnamate-4-hydroxylase (C_4H) converts cinnamate into *p*-hydroxycinnamic acid (Shadle et al. 2007; Bi et al. 2011). Because of double bond in the non-aromatic chain the molecule exists as *trans* isomer. The *trans* to *cis* conversion of CA is known to be regulated and modulated under light in vitro (Kahnt 1967) and root tissues grown in the dark (Locher et al. 1994). Phenylalanine ammonia lyase (PAL) seems to regulate the phenylpropanoid synthesis by feedback inhibition due to *trans*-CA, since partial conversion of *trans*-CA, its derivatives and glucosides to *cis* isomers by UV exposure have been shown to quickly reverse PAL inhibition (Lamb 1979; Mavandad et al. 1990; Sarma et al. 1998). The two main enzymes PAL and C_4H, therefore, have received major attention in phenylpropanoid synthesis, since these ultimately decide the regulation and modulation of flavonoids and other mono- and poly-derivatives of cinnamates. Observations from experiments using sense and antisense transgenics with known activities of PAL and C_4H, and also after subjected to cDNA manipulations, confirmed the earlier observation of negative feedback mechanism of *trans*-CA on PAL enzyme activity (Blount et al. 2000). Further a function alluded to *trans*-CA and phenylpropanoids is that of being photoreceptors since PAL and C_4H activity, as above, is regulated due to an exposure to UV-B (280–320 nm) irradiation (Braun and Tevini 1993). The CA is subsequently converted to various substituted cinnamate derivatives like *p*-coumaric, ferulic, caffeic and sinapic acids (Gang 2005). Further substitutions and modifications of these cinnamate derivatives generate precursors for mono, oligo and polyphenol synthesis such as tannin and lignin (Hahlbrock and Scheel 1989; Ralph et al. 2008; Dos Santos et al. 2008; Zanardo et al. 2009; Vanholme et al. 2010, 2012a, b). The other sources for the synthesis of diverse basic plant phenolic structures and also other aromatic structures are through an acetate pathway (Buchanan et al. 2000). These may be present individually or in combination with the compounds synthesized through shikimate pathway, e.g., large group of flavonoid compounds, chalcones, anthocyanidins/anthocyanins (Lewis and Yamamoto 1990; Boerjan et al. 2003; Hatfield et al. 2008).

Cinnamate isoforms

As mentioned earlier UV irradiation converts *trans*-CA to *cis*-CA which is found in both monocots and dicots (Guo et al. 2011). The biological activity of *cis*-cinnamic acid

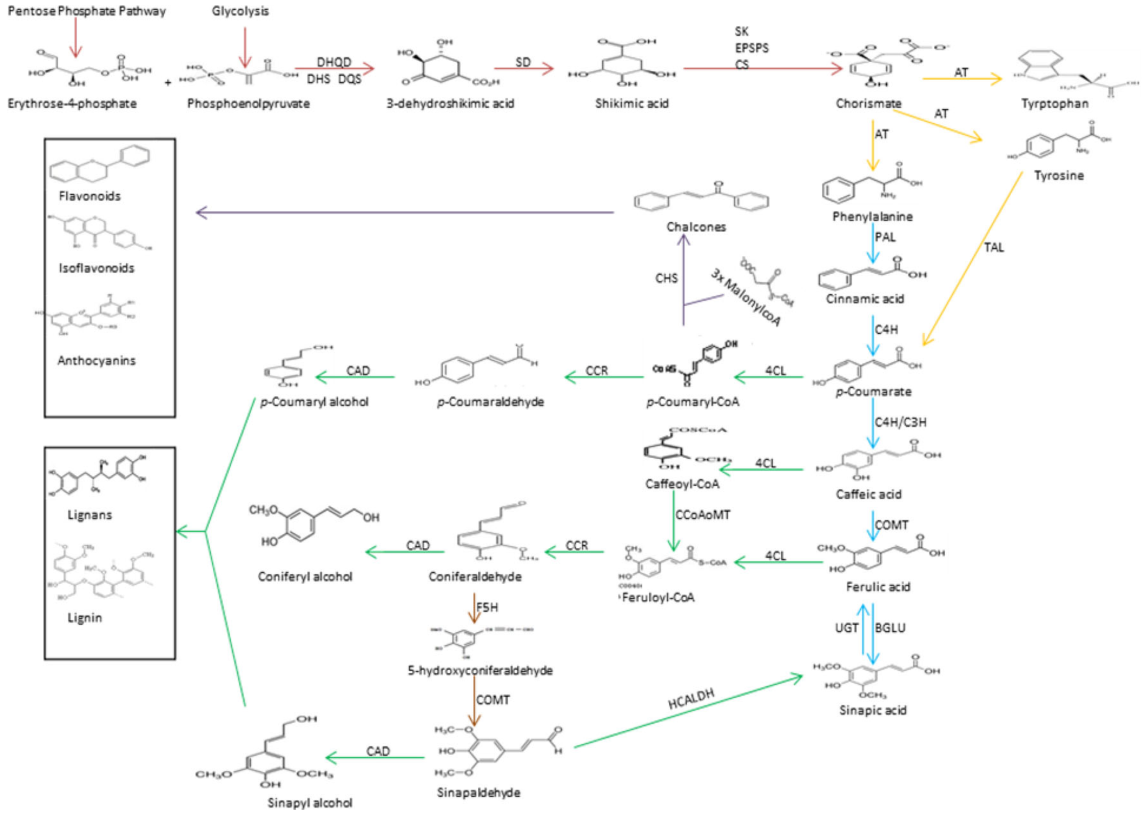

Fig. 1 Biosynthesis and fate of cinnamic acid. *DHS* 3-deoxy-D-arabinoheptulosonate 7-phosphate synthase, *DQS* 3-dehydroquinate synthase, *DHQD* 3-dehydroquinate dehydratase, *SD* shikimate dehydrogenase, *SK* shikimate kinase, *EPSPS* 5-enolpyruvylshikimate-3-phosphate synthase, *CS* chorismate synthase, *AT* amino transferase, *TAL* tyrosine ammonia-lyase, *PAL* phenylalanine ammonia lyase, *C4H* cinnamate 4-hydroxylase, *4CL* 4-coumarate: CoAligase, *C3H* *p*-coumarate 3-hydroxylase, *CCoAOMT* caffeoyl-CoA *O*-methyltransferase, *CCR* cinnamoyl-CoA reductase, *F5H* ferulate 5-hydroxylase, *COMT* caffeic acid *O*-methyltransferase, *CAD* cinnamyl alcohol dehydrogenase, *UGT* UDP-glucosyltransferase, *HCALDH* hydroxyl cinnamaldehyde dehydrogenase, *BGLU* b glucosidase, *CHS* chalcone synthase

(*cis*-CA) was first reported in 1935. An auxin like activity viz. to promote growth in the pea split stem curvature test, the pea segment test and the Avena straight and curvature tests was ascribed to it (Hitchcock 1935; Haagen-Smit and Went 1935). Later *cis*-CA vapors were reported to affect like that of ethylene. Reason being the presence of double bond (HC=CH) in its structure and inducing epinasty in tomato plant (Yang et al. 1999). By employing two mutants of tomato plant, one being deficient in ethylene biosynthesis and the other being deficient in the ethylene perception and after treating these with the vapour of *cis*-CA and ethylene Yang et al. (1999) inferred that the *cis*-CA vapour acts independent of ethylene receptor dependent pathway. They also suggested different action sites for *cis*-CA vapour and ethylene. *cis*-CA, however, has hardly been sourced from plants in nature, except a report for *Alpinia malaccensis* having too meagre amounts to allude to any meaningful physiological activity. This, therefore, almost established it for decades a synthetic plant growth regulator and prompted Zhiqui et al. (2003) to infer that too little determination was devoted to the study of function and production of this plant growth regulator in higher plants. This according to them was, therefore, a cause for very few studies available on its physiological roles. Zhiqui et al. (2003) further on showed the presence of natural *cis*-CA in *Brassica parachinensis* also. They reported that the biosynthesis of *cis*-CA is not well understood, however, suggested possible pathways for *cis*-CA formation viz (1) sunlight-mediated conversion from *trans*-CA, (2) spontaneous conversion from *trans*-CA in the presence of an electron-transfer facilitator, (3) isomerase-mediated conversion from *trans*-CA, and (4) direct enzymatic biosynthesis from L-phenylalanine. Both *cis*-CA and its glucosides are natural products that could be utilized by various indigenous soil organisms.

It is thus likely, as per Hiradate et al. (2005), that *cis*-CA and its glycosides are worth considering as plant growth regulators. These they say are inexpensive to synthesize and also possess a low risk of causing environmental toxicity. However, too little information exists regarding effect of *cis*-CA on PAL enzymatic activity regulation and also its immediate derivatives like *cis-p*-coumaric acid, *cis*-ferulic acid, and *cis*-caffeic acid (Haskins et al. 1964; Wu et al. 2001; Zhiqui et al. 2003) have also been found to be occurring naturally. Yang et al. (1999) demonstrated the biological activities of *cis*-CA in plants. Molecular cloning and subsequent expression of three PAL enzymes (PAL1, PAL2 and PAL4) from *Arabidopsis* have shown that the enzyme activities of these are affected in vitro by the *cis*-CA isomer (Chen et al. 2005). After *trans-CA* was reported by Rovira (1969) being secreted from the roots of guayule (*Parthenium argentatum*) a strong allelopathic plant, the allelopathic potential of *trans*-CA has been further and frequently been reported (Chon et al. 2003; Weir et al. 2004; Macías et al. 2007). *trans*-CA is one of the sole precursor for the biosynthesis of all other phenylpropanoids (Dixon 2001). Horbowicz et al. (2009) reported growth inhibition of primary root of buckwheat by *trans*-cinnamic acid. Since *trans*-CA isomer can be converted into *cis*-CA either by the sunlight or by the presence of an electron-transfer facilitator, it was suggested that the conversion of *trans*-CA into *cis*-CA is involved in the allelopathic phenomenon. This transformation might explain the reported synergism between *trans*-CA and polygodial (Fuzita and Kubo 2003) and abscisic acid (Li et al. 1993). The *trans*-CA treatments have been shown to result in an intracellular release of Ca^{2+} to cytoplasm from the vacuole leading, therefore, to an elevated $[Ca^{2+}]$ cyt level followed by a gradual loss in cell viability of cucumber roots. These results, taken together, were to suggest that $[Ca^{2+}]$ cyt homeostatic disturbance is one of the primary triggers for *trans*-CA phytotoxicity in cucumber (Yu et al. 2009).

Derivatives

CA and its methyl esters and hydroxyl derivatives are *p*-coumaric, ferulic, caffeic and sinapic acids. These constitute important prolifically used components in the industries of flavors, perfumes, synthetic dyes, and pharmaceuticals (Schmidt et al. 1999; Gang 2005; Mahesh et al. 2007; Milkowski and Strack 2010).

p-Coumaric acid

p-Hydroxy-cinnamate being widely distributed throughout the plant kingdom plays important role in plant–insect interactions. Their presence has been identified both in aerial and underground tissues of angiosperms as well as in ferns (Schaefer and Herrmann 1982; Daayf et al. 1997; Wu et al. 1999; Dias et al. 2003). Various orchid species are known to have hydroxyl/methyl-cinnamates, as a component of their floral scent. This, therefore, acts as an attractant for pollinators like euglossine bees (Dodson et al. 1969; Eltz and Lunau 2005). Electro-physiological activity of hydroxyl/methyl-cinnamates towards detached bee antennae has been reported by Eltz and Lunau (2005). Further, leaves of sweet basil (*Ocimum basilicum*) accumulate high levels of hydroxyl/methyl substituted derivatives of cinnamate.

p-Coumaric acid has been reported to suppress the expression of T3SS genes of the plant pathogen *Dickeya dadantii*, through the HrpX/Y two-component system a core regulator of the T3SS, thereby suggesting that by manipulating the expression of the T3SS gene plants can defend against bacterial pathogens. (Li et al. 2009). The ectopic expression of the RsTAL gene encoding TAL, isolated from *Rhodobacter sphaeroides* (RsTAL) a photosynthetic bacterium, when introduced in *Arabidopsis thaliana* enhanced the metabolic flux thereby increasing accumulation of anthocyanins, flavonoids and other phenylpropanoids (Nishiyama et al. 2010).

Ferulic acid

Methyl-*p*-coumarate (ferulic acid) shows high levels of insecticidal cum insect-deterrent (Winkel-Shirley 2002) and also antifungal properties (Seifert and Unger 1994). Daayf et al. (1997) suggested that ferulate acts as an anticipin and an elicitor-inducible phytoalexin in *Cucumis sativus.* Lipid peroxidation is a major oxidative process of food spoilage and ferulic acid inhibits spoilage by inhibiting fatty acid peroxidation (Kanski et al. 2002). The ferulate esters are substituted cinnamate intermediates synthesized to be transported as cell wall components and also suberin biosynthesis (Mir Derikvand et al. 2008) and of suberins (Soler et al. 2007; Molina et al. 2009; Rautengarten et al. 2012). In grasses (monocots) the ferulate-polysaccharide esters have been shown to have well-established roles in polysaccharide–polysaccharide bridging and lignin–polysaccharide cross linking (Ralph et al. 1994a, b, 1998, 2010; Hatfield et al. 1999; Grabber et al. 2000). It is, therefore, suggested that ferulate esters may be acting as induction sites for cell wall lignification (Ralph et al. 1995; Grabber et al. 2002) and are therefore of a common presence in the rice, wheat, oats and sweet corn (Sri et al. 2003).

Sweet basil (*Ocimum basilicum*) has interestingly been shown as an excellent system for investigating the methyl cinnamate and methyl-*p*-coumarate (ferulate) production in plants. The glandular trichomes in basil are metabolically super active entities producing large amounts of terpenoids, phenylpropanoids and various fatty acid derivatives (acetate pathway for aromatic compound synthesis) (Iijima et al. 2004a, b). These secretory trichomes synthesize a battery of secondary compounds after diverting intermediates from major primary pathways to secondary pathways; which include the synthesis of abundance of volatile compounds also. Several basil lines, producing differential quantities of compounds through these pathways, especially volatile and aromatic compounds have been developed (Iijima et al. 2004a, b). One of the lines known as cinnamon basil (line MC) is reported for its production of methyl cinnamate in sizable amounts (Iijima et al. 2004a, b) by the activity of a novel carboxyl methyl-transferase designated as *p*-coumaric/cinnamic acid carboxyl methyltransferase (CCMT).

Caffeic acid

Caffeic acid is another naturally occurring cinnamate derivative reported in many fruits, vegetables, and other plants, in varying amounts depending upon the plant and its species (Chung et al. 2004). It is also reported in the coffee plant (Chung et al. 2004). Caffeic acid is a 5-*p*-coumarate or 3, 4 dihydroxy cinnamate and is implicated prominently in preventing DNA single-strand breakages and cytotoxicity (Sestili et al. 2002). Caffeic acid is a metabolite of the phenylpropanoid pathway found in several plant species, weed residues (Weir et al. 2004) and soils (Siqueira et al. 1991). It has been reported to induce changes in seedling emergence (Miller et al. 1991), rhizogenesis (Batish et al. 2008), evapo-transpiration (Blum and Gerig 2005), photosynthesis (Barkosky et al. 2000) and root growth (Baleroni et al. 2000). Caffeic acid have also been shown to inhibit the root length and fresh and dry weights of different plant species, such as soybean seedlings (Bubna et al. 2011), mung bean (Batish et al. 2008), *Arabidopsis thaliana* (Reigosa and Pazos-Malvido 2007), canola (Baleroni et al. 2000) and pea (Vaughan and Ord 1990). Caffeic acid affects morphogenetic response of hypocotyl cutting and early growth of mung bean (Batish et al. 2008), thus also proving its phytotoxicity. Caffeic acid is reported to generate an increase in activities of soluble peroxidase along with other antioxidant enzymes (i.e., superoxide dismutase, ascorbate peroxidase, glutathione reductase and catalase) in the mung bean hypocotyl (Batish et al. 2008; Singh et al. 2009). Exogenously applied caffeic acid decreased the PAL activity and hydrogen peroxide content and increase the soluble and cell wall bound peroxidase activities. Caffeic acid in conjugation with piperonylic acid (PIP, an inhibitor of the cinnamate 4-hydroxylase), equalized the inhibitory effect of PIP, whereas with methylene dioxocinnamic acid (MDCA, an inhibitor of the 4-coumarate:CoA liogase, 4CL) lignin production is decreased. This indicated that exogenously applied caffeic acid can be channeled into the phenylpropanoid pathway via the 4CL reaction, by resulting lignin monomers increase thereby solidifying the cell wall and thus inhibiting root growth (Bubna et al. 2011). Caffeic acid biosynthesis from cinnamic acid via *p*-coumaric acid involves plant-specific cytochrome P450 dependent monooxygenase enzymes, cinnamate 4-hydroxylase (C4H) and *p*-coumarate 3-hydroxylase (C3H) (Kim et al. 2011). Berner et al. 2006 reported in actinomycete *Saccharothrix espanaensis* that the biosynthetic pathway for *trans* caffeic acid from L-tyrosine via *trans*—*p*-coumaric acid involves the co-expression of sam5 and sam8 genes. The heterologous expression of sam8, encoding tyrosine ammonia lyase, led to the biosynthesis of *p*-coumarate and the sam5 encoding *p*-coumarate 3-hydroxylase, producing *trans*-caffeic acid.

Sinapic acid

Sinapic acid, a phenylpropanoid compound with 3, 5-dimethoxyl and 4-hydroxyl substitutions in the phenyl group of cinnamate, has been found in various high-bran cereals and herbal materials and constitutes over 73 % of the free phenolic acids (KozBowska et al. 1990). It is present in variety of foods, fruits and edible plants (Shahidi and Naczk 1995; Thiyama et al. 2006) particularly in broccoli, citrus juices and leafy brassicas (Stevanovic et al. 2009). It has anxiolytic cum anti-inflammatory properties and has been proposed as an efficient antioxidant (Yoon et al. 2007; Yun et al. 2008). With the exception of its antioxidant activities (Niwa et al. 1999; Kikuzaki et al. 2002; Akhter et al. 2003) its pharmacological properties have rarely been reported (Yoon et al. 2007). Sinapate esters (e.g., sinapoyl malate and Sinapoyl glucose) act as UV protectants in *Brassicaceae* and the genes involved in their biosynthesis in *Arabidopsis* are well described (Fraser et al. 2007; Sinlapadech et al. 2007). Sinapoyl malate has been suggested to act as a foliar UV protectant in *Arabidopsis* (Landry et al. 1995). The pathway for sinapoyl malate biosynthetic in the *Brassicaceae* is well characterized biochemically (Strack 1977), and *Arabidopsis* genes encoding the enzymes upstream and downstream of UDP-glucosyltransferase (UGT) involvement have been identified by mutational analysis (Lorenzen et al. 1996). Study of the fah1-mutant of *Arabidopsis* defective in the accumulation of sinapic acid-derived metabolites, including guaiacyl–syringyl showed that the seedlings were more susceptible than wild type to UV stress (Landry et al. 1995). Since the fah1; being locus of *Arabidopsis* which encodes the ferulate-5-hydroxylase (F5H) enzyme that catalyzes the rate-limiting step in syringyl lignin biosynthesis and is required for the production of sinapate esters. It is a cytochrome P_{450}-dependent monooxygenase responsible for the formation of 5-hydroyferulic acid, the precursor of sinapic acid (Chapple et al. 1992; Ruegger et al. 1999) and the product of the reaction, 5-hydroxyferulic acid, or metabolites downstream of 5-hydroxyferulic acid, such as sinapic acid and sinapoyl malate, were involved in UV protection. However, recent analysis of *Arabidopsis* over expression fah1 have shown no accumulation of sinapoyl malate (Ruegger et al. 1999), suggesting that levels of fah1 do not control flux through this part of the cinnamate pathway. Since the glucose ester is the direct precursor of sinapoyl malate, manipulation of the UGT levels involved in its formation may provide a better tool to investigate the potential link between sinapoyl malate and UV protection (Lim et al. 2001). Niwa et al. 1999 and Zou et al. 2002 have reported the strong inhibition in peroxynitrite mediated oxidation due to scavenging activity of sinapic acid. Sinapic acid isolated from *Brassicca juncea* has been reported to be an inhibitor of the production of serum protein nitration and low density lipoprotein lipid per oxidation (Zou et al. 2002).

Conclusion

Within the last few decades, strong evidence supporting the role of phenolic compounds in the growth and development of plants has been published. The presence of cinnamic acid, alpha beta unsaturated acid, an ubiquitous plant phenol and its derivatives is an enough indication that these have been adopted by plants for various mechanisms. Better understanding of these diverse groups in plants will eventually help in modelling sustainable plant growth and development.

Author contribution statement Razia Shuab and Rafiq Lone have done the literature collection and prepared the manuscript and K. K. Koul has put the manuscript in final shape.

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